



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE CLIMAX FOREST OF ISLE ROYALE, LAKE SUPERIOR, AND ITS DEVELOPMENT. III

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 165

WILLIAM S. COOPER

(WITH TWENTY-FIVE FIGURES)

The hydrarch successions

The bog succession

I. Physiographic development of the bog habitat

At the commencement of the glacial period the topography and the drainage system of what is now Isle Royale were very similar to those of today, except that lakes and swamps were few or absent. This topography was but slightly modified by the invasion of the ice, and the most important change effected by glacial erosion was the excavation of rock basins in the preglacial valleys. Since the retreat of the ice the gradual emergence of the island from the waters of the lake has taken place. In some cases inclosed basins appeared above the surface ready made; in others they were produced by wave-built bars thrown across the mouths of harbors or both ends of channels during pauses in the retreat of the waters. By continued emergence some of these rock basins and cut-off bays came to occupy positions far in the interior of the island. The tilting which followed the Lake Nipissing stage must have had some effect upon the island lakes thus formed. It may have brought about the partial draining of some, the enlargement and perhaps even origination of others, and occasional shifting of outlets; in all cases it must have produced a tendency toward migration to the southwest.

The physiographic development of the bog habitat thus includes as a rule two periods: first, the channel-bay stage, and second, the lake stage. Numerous localities that illustrate the process may be seen today, especially at the northeast end of the island. Duncan

Bay would become a lake if the water level should sink 5-6 m.; Pickerel Cove is a similar case; and the inland portion of Rock Harbor is nearly closed at its narrowest point by a sand bar that has been built almost to the surface.

Several of the lakes of Isle Royale are of respectable size. Siskowit Lake, the largest, is more than 10 km. long and 2.5 km. wide (fig. 31). The majority are small, many being mere ponds.

All the lakes, and the harbors as well, are tending toward extinction through down-cutting of outlets, sedimentation, and vegetation. Down-cutting of outlets has as yet accomplished very



FIG. 31.—Siskowit Lake: the largest of the Isle Royale lakes

little. The large lakes like Siskowit are being filled by sedimentation with extreme slowness, because of the small size of the streams, their slight gradient, and the thick covering of vegetation which almost inhibits erosion of the land surfaces. It is impossible for bog vegetation to obtain a foothold in the large lake basins except here and there in very sheltered spots, because of vigorous wave and ice action (HOLT 33, p. 218). They will therefore remain much as they are for a long time. In the small lakes, on the other hand, where wave and ice action are not severe, invasion by bog vegetation is in active progress.

II. Vegetational development in the bog habitat

1. Channel-bay stage

Even as early as the channel-bay stage we find the beginnings of the vegetational history of the bog habitat. If the body of water be large or subject to considerable wave and current action, plant life is practically absent. In sheltered places, however, there lives a plant society, sparse but characteristic. The commonest species is *Isoetes macrospora* Dur. (quillwort), growing entirely submerged at a depth of 0.3–1 m. in the silty sediment that covers the bottom. *Isoetes* here attains an unusual size, the crowns being frequently 5 cm. and more in diameter. With it grow occasional plants of *Chara* (stonewort), *Ranunculus aquatilis* L. var. *capillaceus* DC (water crowfoot), *Potamogeton perfoliatus* L. and other spp. (pondweeds). On shoals and along the reefs at the ends of the narrow islands and points are frequent clumps of sedges: *Carex aquatilis* Wahlenb., *C. stricta* Lam., *C. lenticularis* Michx.

2. Lake stage

The lake stage is considered as extending from the first complete inclosure of the body of water to the time when the bog vegetation has brought about its extinction. During this physiographic stage all the vegetational stages of the bog succession usually appear in their accustomed order. The aquatics are already present and the sedge society has often made a slight beginning. The latter now develops with rapidity, especially in the smaller lakes, and is followed in turn by the sphagnum-shrub society and the bog forest.

a) Peat formation

Peat formation in the northern and southern peninsulas of Michigan has been described by TRANSEAU (56) and by DAVIS (19). The bogs which DAVIS studied, especially in the Upper Peninsula, are very similar to those of Isle Royale, and this author shows that the sedge mat is the most important agent in the formation of the peat. Lack of time and facilities prevented a study of the basin-filling process upon Isle Royale, but it is certain that the bulk of the peat is deposited through the formation and sinking of the sedge mat and the accumulation of finely divided material

dropped from it. A subordinate amount is formed from the remains of the aquatic vegetation preceding the sedges in the invasion of the basins and from the shrub-sphagnum vegetation which follows them.

b) Illustrative localities

To illustrate the course of the bog succession upon Isle Royale several representative localities will be briefly described. Amygdaloid Lake shows the bog plants gaining their first foothold along the shore; the two ponds near Tobin's Harbor have been partially



FIG. 32.—Amygdaloid Lake: in the foreground a thick growth of *Menyanthes* and *Lysimachia thyrsiflora*; farther out, *Nymphaea advena*.

covered and filled; and the basin on Raspberry Island contains a completely covered bog.

Amygdaloid Lake (fig. 32).—Amygdaloid Island lies parallel to the northwest shore of Isle Royale and is formed by two partially submerged ridges of the usual kind. Between the ridges is an inclosed basin which contains a narrow lake, 100 m. wide at the most, but 1.2 km. long. It should be noted that Amygdaloid Lake is identically like the basin on Raspberry Island, to be described later, in situation and physiographic development. For some reason its history has not progressed so far, although both are at

the present lake level. It may be that the basin has been more recently shut off from Lake Superior than that on Raspberry Island, and also the depression is larger and doubtless deeper. The climax forest descends to the edge of the interior lake, except for an occasional short strip of stony or sandy beach. At the southwest end there is a considerable amount of bog vegetation, growing in water a few centimeters deep and underlain by 2 m. of soft mud containing much organic material. The principal aquatic is *Nymphaea advena* Ait. (yellow pond lily). There is next a zone of amphibious plants dominated by *Menyanthes trifoliata* L. (buckbean), which is accompanied by *Lysimachia thyrsiflora* L. (bog loosestrife) and a few other species. As will be noted later, *Menyanthes* is frequently an important mat-former. Through the middle of this zone winds a narrow streamlike ribbon of water, probably the last remnant of a sluggish outlet. Back of the *Menyanthes* zone and filling the continuation of the basin for 0.5 km. is the bog forest, composed of *Larix* and *Picea mariana*, with *Alnus incana* (L.) Moench (hoary alder) in front.

The arrangement of the vegetation here illustrates a feature characteristic of the bog-filled depressions of Isle Royale. On account of the elongated form of the basins, the building out of the bog vegetation goes on much more rapidly at the ends of the lakes than along their sides, because of gentler slope. Theoretically, also, it should build out faster on the northwest side than on the southeast, since by reason of the rock structure the former slope is normally gentler than the latter. In a few cases notable difference was seen in the width of the sedge mat corresponding to the difference in slope, but usually the width of the zone on the two sides was about the same. Probably talus deposits, slope wash, and sediments of various kinds tend to lessen the slope of the southeast side, making it more or less equal to that of the other.

It has been stated that along the greater part of the lake shore the climax forest descends to the water's edge. At one point (a sandy stretch) bog vegetation was found to be obtaining its first foothold. Farthest out were scattering plants of *Nymphaea advena*. Close to shore grew scattered stools of *Carex filiformis* L. (bog sedge) and plants of *Eleocharis palustris* (L.) R. & S. (creeping

spike-rush) and *Equisetum fluviatile* L. (scouring rush). Here we have the very beginning of the sedge mat, *Carex filiformis* being the most important mat-builder in most of the Isle Royale bogs. Next came a nearly bare level sandy shore 1-3 m. wide, at the upper edge of which began a second belt of bog vegetation. A line of depauperate *Menyanthes* with rootstocks creeping out over the gravel formed the lowest portion. It is probable that there has been a slight recent change of level in Amygdaloid Lake and that the *Menyanthes* marks the height of the former water surface. Above the *Menyanthes* was an area peopled by a number of species belonging partly to the bog forest and partly to the climax forest. These are as follows: *Lycopodium annotinum* L. (stiff club moss), *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Chiogenes hispidula* (L.) T. & G. (snowberry), *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage), *Coptis trifolia* (L.) Salisb. (goldthread), *Linnaea borealis* L. var. *americana* (Forbes) Rehder (twin-flower), *Pyrola secunda* L. (shin leaf), *Cornus canadensis* L. (bunch-berry), *Trientalis americana* (Pers.) Pursh (star-flower), *Maianthemum canadense* Desf. (two-leaved Solomon's seal), *Mitella nuda* L. (mitrewort), *Moneses uniflora* (L.) Gray (one-flowered wintergreen).

This low vegetation was nearly smothered by a dense growth of sphagnum, much of it very young. The *Lycopodium*, which was the most abundant species of the list given above, showed only the tips of its branches except along the edge of the sphagnum mass, where thick clusters of new shoots projected from beneath the moss. The plants of *Coptis* were many of them buried up to the leaves. Upon the surface of the sphagnum grew *Drosera rotundifolia* L. (sundew) and *Linnaea*. A low beach ridge supported the most luxuriant sphagnum growth, which was occasionally as much as 0.3 m. deep, especially where it surrounded shrubs and tall grasses. *Calamagrostis canadensis* (Michx.) Beauv., *Agrostis hyemalis* (Walt.) BSP, *Iris versicolor* L., *Campanula uliginosa* Rydb. (bog bell-flower) grew here, and also *Alnus incana* (L.) Moench. (hoary alder). It is noteworthy that everywhere along the shore, except where the sphagnum has become established, *Alnus crispa* rather than *A. incana* forms the forest margin. In and around the sphagnum grew a few bog trees, *Larix* 1-3 m. in height, and young

Picea mariana and *Thuja*; and back of these was a narrow band of bog forest, hardly more than a single line of large trees, *Larix* and *Thuja*, with much young *Abies* and *Betula*, and the usual herbaceous growth of such a habitat, practically the list given above. The sphagnum was evidently spreading from the ridge both toward the water and into this area of bog forest. Behind all was the climax forest of balsam, spruce, and birch.

It is evident from the foregoing description that at this locality we have in embryo every society or zone of the bog succession,



FIG. 33.—Sucker Lake: aquatics; sedge zone of *Carex filiformis* type, fringed with *Menyanthes*; at the left a narrow zone of shrubs and a thin line of tamaracks bordering the climax forest; a thick growth of bog trees at the end of the basin (distance).

from the aquatics through the sedge mat (represented by the stools of *Carex* and its companions), the sphagnum-shrub zone supporting the nascent bog forest, to the mature bog forest invaded by the climax trees; and all in the space of only 10 m. It is thus demonstrated that all the zones may begin their development at approximately the same time.

Sucker Lake (fig. 33; Sec. 34, T. 67 N., R. 33 W.).—The development of the bog vegetation is here far advanced. A wide zone of aquatics nearly surrounds the small area of open water, and this in turn is surrounded on three sides by a broad sedge mat made up of

Carex filiformis L., *C. limosa* L., *C. chordorrhiza* L. f., *C. polygama* Schkuhr, *C. oligosperma* Michx., and *C. livida* (Wahlenb.) Willd. Along the outer edge of the mat and almost forming a zone by itself is a fringe of *Menyanthes*, its thick rootstocks closely intertwined. The shrub zone, dominantly *Myrica Gale* L. (sweet gale), is poorly developed, and sphagnum is nearly absent, only a sparse growth being seen and this nearly choked by the luxuriant sedges. Along much of the southeast shore the sedge mat is absent and the shrubs are the marginal vegetation. Here *Chamaedaphne* and



FIG. 34.—Pond near Tobin's Harbor in Sec. 5, T. 66 N., R. 33 W.: aquatics occupying center; sedge zone of *Carex filiformis* type; in the background hoary alder and tamaracks bordering the climax forest.

Andromeda grow actually in the water. DAVIS (19) has noted this replacement of the sedge zone by a shrub mat as a very common occurrence in the bogs of the northern peninsula of Michigan, but it is rare on Isle Royale. The bog forest at Sucker Lake is a mere line of tamaracks along the sides of the basin, but is well developed at both ends, where great stretches of the narrow depression have been converted into a forested valley. Sucker Lake is the last remnant of a body of water that was once very similar to the Rock Harbor of today.

Pond near Tobin's Harbor (fig. 34; Sec. 5, T. 66 N., R. 33 W.).—This locality is closely similar to the last and occupies the same type of basin, with considerable bog forest at both ends. Development has proceeded one step farther, there being no open water, and the aquatics thus occupy the center. The sedge zone is continuous and everywhere equally developed. Soundings through the mat showed that the slopes of the bottom on the northwest and southeast sides are not notably different. *Carex filiformis* is the principal mat-former. The other species contributing are *Carex*



FIG. 35.—Same locality as fig. 34: *Scirpus hudsonianus* prominent in the sedge zone: islands of shrubs, *Alnus incana* surrounded by *Chamaedaphne*; a thick growth of bog trees at the end of the basin.

limosa L., *C. chordorrhiza* L. f., *C. Michauxiana* Boechl., *C. livida* (Wahlenb.) Willd., and *C. polygama* Schkuhr. The principal bog herbs accompanying the sedges are as follows: *Menyanthes trifoliata* L. (buckbean), *Potentilla palustris* (L.) Scop. (marsh cinquefoil), *Vaccinium Oxycoccus* L. var. *intermedium* Gray (cranberry), *Rhynchospora alba* (L.) Vahl (white beak-rush), *Cicuta bulbifera* L. (water hemlock), *Hypericum virginicum* L. (marsh St. Johnswort), *Scirpus hudsonianus* (Michx.) Fernald (alpine cotton-grass), *Epilobium palustre* L. (marsh willow-herb), *Scutellaria galericulata*

L. (skull-cap), *Lysimachia terrestris* (L.) BSP (loosestrife), *Campanula uliginosa* Rydb. (bog bell-flower), *Galium Claytoni* Michx. (bedstraw), *Lycopus uniflorus* Michx. (bugle-weed), *Sarracenia purpurea* L. (pitcher-plant), *Drosera rotundifolia* L. (round-leaved sundew), *Iris versicolor* L., *Arethusa bulbosa* L., *Spiranthes Romanzoffiana* Cham. (lady's tresses), *Habenaria dilatata* (Pursh) Gray (white bog orchis), *H. psycodes* (L.) Sw. (purple-fringed orchis). *Sphagnum* is rare. The shrub zone is better developed than at Sucker Lake and includes two subzones: the outer, in which *Chamaedaphne calyculata* (L.) Moench is dominant and accompanied by *Andromeda glaucophylla* Link and *Salix pedicellaris* Pursh; the inner, of *Alnus incana* (L.) Moench. Advance islands of shrubs are scattered here and there over the sedge mat, the outermost being composed of *Chamaedaphne*, and the inner of a nucleus of *Alnus incana* surrounded by a circular zone of *Chamaedaphne* (fig. 35). Seedlings of tamarack are frequent in these colonies. The subzone of *Alnus incana* fringes the outer edge of the bog forest, which here as usual is a mere line along the sides, but broader at the ends. The bog tree is the tamarack.

3. Open bog stage: Raspberry Island bog

Raspberry Island is one of the row that bounds Rock Harbor on the southeast, and is next in line to Smithwick Island, studied in connection with the climax forest. Its upland forest cover was originally like that of Smithwick, but unfortunately this has been largely fire-swept, the bog area, however, having escaped unharmed. The island consists of two parallel ridges of the typical Isle Royale kind, bounding a narrow depression, closed at both ends by beach ridges, which contains the bog area. The outer ridge is the more massive of the two and makes the bulk of the island, while the inner is only half as long. Both reach an elevation of about 10 m. The island has emerged from the lake in comparatively recent time, and its history has been a simple one; moreover it is in all essentials the history of Isle Royale itself on a small scale. When the lake level was 3 m. higher than now there was a channel over the site of the bog area. At this time currents and waves were doubtless at work building bars across the channel mouths. With continued sub-

sidence of the lake level the bar at the exposed southwest end emerged and became a beach connecting the two ridges, which now inclosed a sheltered bay. Into this considerable sediment was still being carried by waves and currents. As the lake level continued to fall, the more slowly building bar across the sheltered northeast end of the harbor emerged, and the bay was now an inland lake. It is probable that the height of both beaches has been increased since their emergence through the agency of storm waves. The physiographic history of the habitat is thus concluded. Its likeness to Amygdaloid Island will be at once evident. At Amygdaloid Lake we find the beginnings of the bog vegetation; Raspberry Island shows its culmination, in the sense that at this stage the open water has disappeared, and all the bog societies are present and at their best development. The further history will record the progressive extinction of these societies by centripetal invasion.

The relations of the zones to each other are shown in the

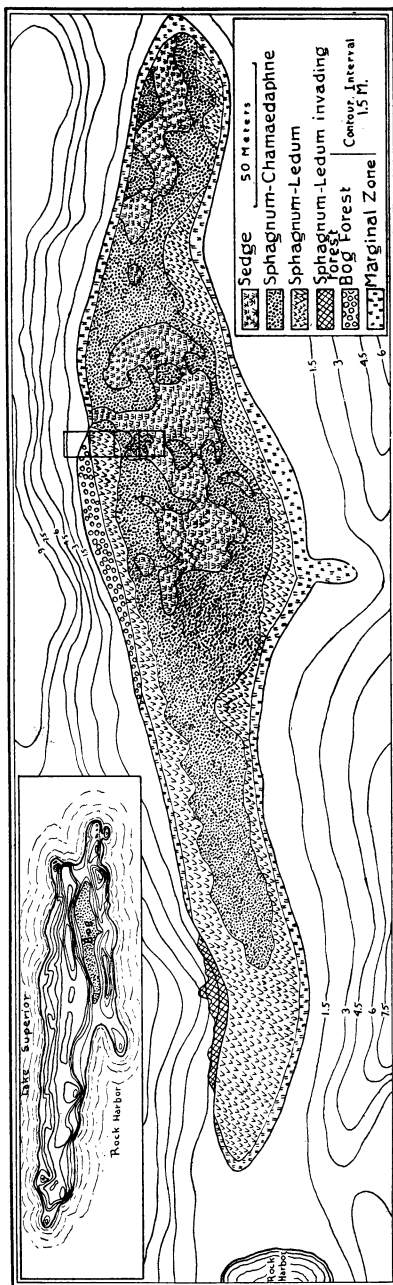


FIG. 36.—Map of Raspberry Island (upper left-hand corner) and the bog area on a larger scale: the location of quadrat 9 is shown

map (fig. 36) and in the general view (fig. 37). Certain features of the succession were so well developed in this bog that they must have a place in this account.

The sedge mat is composed almost entirely of *Carex limosa* L. (mud sedge) (fig. 38). Occasional bare muddy spots are nearly free of sedge, but support a scattered growth of *Menyanthes* and *Drosera anglica* Huds. (narrow-leaved sundew). These appear to represent the youngest stage now existing in this habitat.



FIG. 37.—Raspberry Island bog: general view; sedge zone of *Carex limosa* type in the foreground; the sphagnum-shrub society occupies most of the view; young bog trees as pioneers of the forest; black spruce prominent in the bog forest.

a) The sphagnum and its relations

Particular attention was given to the sphagnum, which is very luxuriant in this bog; especially to its point of origin, the conditions governing its spread, and its relations to companion species.

The first point to be noted is that the sphagnum is a superficial layer supported upon the sedge mat, and thus does not contribute in any large degree to peat formation. This feature has been noted by HOLT (33) for the Isle Royale bogs, and by TRANSEAU (56) and DAVIS (19) for the northern and southern peninsulas of Michigan.

The next important fact is that the sphagnum does not make its first growth at the extreme edge of the bog area and from here works its way centerward only. On the contrary, it begins its growth some distance within the bog margin and works both ways; very slowly toward the margin, faster toward the center. Proof of this course of events is seen in the entire absence of sphagnum from the marginal zone, except in certain parts where it is manifestly a recent invader. Soil samples taken at various depths in



FIG. 38.—Sedge zone of *Carex limosa* type; Raspberry Island

the marginal zone, examined microscopically, failed to show the slightest trace of sphagnum remains, although these are long preserved and readily recognized. Another proof is found in the form of the sphagnum accumulation, which is that of a ridge parallel to the bog margin and at a somewhat constant distance from it. This ridge usually has its greatest thickness close to the outer (marginal) side, doubtless marking here the region of first growth. It will be remembered too that in the primitive stage observed at Amygdaloid Lake the sphagnum was seen to be spreading both ways. The face toward the bog margin (on Raspberry Island) is usually rather abrupt, forming a prominent wall which bounds the marginal zone. Occasionally a thin layer of sphagnum is found

to be invading the latter area. In the opposite direction (centerward) the sphagnum decreases *gradually* in thickness, and at its edge invasion of the sedge zone is actively taking place. Fig. 39, drawn to scale, is a typical bog section. The form of the ridge is shown and also the depth at various points. The high projection upon the sphagnum mass is a hummock, the true marginal face being at the right. A tongue of the moss is seen invading the marginal zone. Below the line which is drawn as marking the base of the sphagnum the soil is black peat containing little that is recognizable even with a microscope. At several places, however, sphagnum fragments were recognized in various degrees of abundance some centimeters below the line indicated. These were

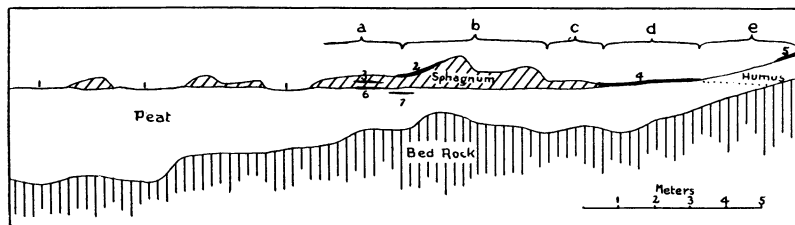


FIG. 39.—Section through Raspberry Island bog: *a*, *Sphagnum-Chamaedaphne*; *b*, *Sphagnum-Ledum*; *c*, *Sphagnum* invading marginal trench; *d*, marginal trench; *e*, upland; 1, sedge zone; 2, *Calliergon Schreberi*; 3, *Calliergon Schreberi* (fossils); 4, *Carex trisperma* and *Hylocomium proliferum*; 5, *Hylocomium proliferum*; 6, 7, *Drepanocladus vernicosus* (?) (fossils).

probably washed down from above, since this line certainly indicates the plane at which the growth began.

The development of the sphagnum has not made uninterrupted progress, for at 3 on the section a stratum was found which contained abundant fragments of *Calliergon Schreberi*, and at 6 and 7 remains of *Drepanocladus vernicosus* (Lindb.) Warnst. were discovered. These two species evidently obtained a foothold upon the surface of the sphagnum and for a time arrested its growth over certain areas. The latter again gained the upper hand and buried the invaders.

The zone included between the sphagnum and the slopes of the upland commonly takes the form of a circular trench. This "marginal trench" is a widespread feature of bogs, and various

causes for its occurrence have been suggested by MACMILLAN (38), SHAW (52), DAVIS (19), and ATKINSON (5). None of these explanations could be applied with certainty to the phenomenon as observed upon Isle Royale, but that offered by ATKINSON seemed most plausible, that is, that during the early development of the sedge mat the sphagnum was excluded by the shade cast by the near-by forest growth. Only after the bog substratum had built out beyond the shaded area did the moss become established upon it.



FIG. 40.—Tension zone between sedge and sphagnum-shrub societies: *Carex limosa* and *Chamaedaphne* keep pace with the growth of the sphagnum by upward elongation; Raspberry Island.

The third point to be considered is the manner of invasion by the sphagnum, including its relations to the sedges and other plants which it finally replaces, and to the shrubs which accompany or follow it. The sphagnum area spreads marginally, and at the same time colonies of young plants originate among the sedges in advance of the main mass. Several such colonies are shown on the map (fig. 36). By the coalescence of these and the solid mass behind, the sphagnum zone extends itself at the expense of the sedge mat.

Certain plants of the sedge zone persist for some time after the sphagnum has gained control. They do this by a process of upward

elongation, keeping pace in this way with the building up of the moss. *Carex limosa* itself survives for a considerable time. Stalks of this species apparently growing on the sphagnum can always be traced down to the stratum beneath, and the buried portions are found to be covered with dead remnants of leaves (fig. 40). *Menthanthes* manages to persist for a time in a similar way. *Saracenia*, which as a rule precedes the sphagnum, makes use of the same method in an endeavor to hold its own, but is less successful



FIG. 41.—Zonal arrangement of bog shrubs: *Andromeda* in the foreground, mainly upon the sedge mat; *Chamaedaphne* (middle ground at the right) mainly upon a mound of sphagnum; Raspberry Island.

and is soon buried. Certain of the bog shrubs belong to the same class. *Chamaedaphne*, *Andromeda*, and *Salix pedicellaris* usually precede the sphagnum. When the moss starts its growth in the vicinity of these plants it builds up rapidly around their stems, forming the hummocks that are so characteristic of sphagnum bogs. Of the three shrubs, *Chamaedaphne* has the greatest power of holding its own against the smothering tendency of the moss (fig. 40); the willow is next; while *Andromeda* soon succumbs.

The two important bog shrubs, *Andromeda* and *Chamaedaphne*, are zonally arranged (fig. 41). *Andromeda* grows freely on the sedge mat, especially in the wetter parts, is most abundant just at the

edge of the sphagnum, and occurs to a limited extent some distance back in the moss. *Chamaedaphne* is also found commonly upon the sedge mat, but inhabits the drier portions. In the sphagnum area it is abundant and over a wide belt almost the only shrub, extending back until it meets the zone where *Ledum groenlandicum* is the dominant species. Relative ability to withstand extreme wet bog soil conditions determines this zonation at the beginning, but the sudden elimination of *Andromeda*, leaving *Chamaedaphne* in full control, is due principally to the smothering effect of the sphagnum, which the former shrub is unable to avoid. *Chamaedaphne*, on the other hand, is able to grow up with the moss indefinitely, and therefore persists until the entrance of *Ledum* introduces a new factor. It is not certain that *Chamaedaphne* does not sometimes germinate upon the surface of the sphagnum as well as upon the sedge mat, and thus in part maintain its dominance. It is certain, however, that *Andromeda* does not commonly do so, at least not successfully. Two other shrubs, *Kalmia polifolia* Wang (pale laurel) and *Betula pumila* L. (dwarf birch), occur in this and other bogs, but not in sufficient abundance for satisfactory study of their habits.

Upon the surface of the sphagnum another group of species becomes established. Important among these are *Carex pauciflora* Lightf., *Smilacina trifolia* (L.) Desf. (three-leaved Solomon's seal), *Drosera rotundifolia* L. (round-leaved sundew), *Vaccinium Oxycoccos* L. (small cranberry). All of these are able in greater or less degree to keep pace with the continued upward growth of the moss.

Of far greater importance than these is *Ledum groenlandicum* Oeder (Labrador tea), which becomes established long after the other shrubs, indeed after all but *Chamaedaphne*, have disappeared. *Ledum* is almost invariably found to be related definitely to the sphagnum, its whole root system being contained within the mass. The growth that it forms is very dense (fig. 42), and as it is a taller shrub than *Chamaedaphne* it shades it severely, and thus finally causes its elimination. Its effect upon the sphagnum is similar. Because of the shade which *Ledum* produces and the considerable amount of waste which falls from it, the upward growth of the moss is gradually retarded and finally ceases altogether.

About this time or often before, young plants of other mosses more or less tolerant of shade become established upon the higher parts of the sphagnum mass. *Polytrichum strictum* Banks is the first arrival, and *Aulacomnium palustre* (L.) Schwaegr. and *Calliergon Schreberi* (Willd.) Grout soon follow. These species form mats of continually increasing lateral extent, which put an effectual stop to further upward growth of sphagnum.



FIG. 42.—*Sphagnum-Ledum* zone, the moss entirely concealed by the abundant growth of the latter; the edge of the bog forest in the background; Raspberry Island.

b) Sphagnum invading the forest

The fact has been mentioned that the sphagnum frequently spreads into the marginal zone as well as toward the center of the bog. In some places this invasion is so effective that the marginal zone is entirely obliterated. The moss does not always stop even here, but occasionally climbs entirely out of the bog, invading the climax forest. A case of this kind was reported by HOLT (33) from a locality near Siskowit Lake. A far more striking instance was discovered on Raspberry Island, near the northeast end of the bog (see map, fig. 36 and fig. 43). In a stretch of 50 m. along the margin the sphagnum had completely obliterated the marginal zone and had ascended the slope for varying distances. At the point of

farthest advance the mass had taken the form of a tongue 4 m. wide, extending 10 m. from the true bog margin. The slope of its surface was about 25° and the highest point reached was 4.5 m. above the bog level. The sphagnum supported a luxuriant growth of *Ledum* which completely covered it. The unusual abundance of flowers in comparison with the plants of the bog itself was a noteworthy feature, as was also the comparatively small size of the leaves, both facts perhaps indicating somewhat hard conditions. *Vaccinium Oxycoccus* and *Chiogenes hispidula* were also abundant, and frequent small seedlings of birch, black spruce, and balsam were found. The depth of the moss was 0.6-1 m., and the edges were abrupt, but unfortunately the fire which destroyed the upland forest had encroached somewhat upon the bog vegetation, so that the marginal conditions could not be ascertained.

4. The bog forest and its development

Although in the Raspberry Island locality the bog forest is not so extensively developed as in other places, all the essential features are present. A series of four adjoining units was laid out, each 5 m. square, the whole forming a broad section cutting through all the societies from the sedge zone to the climax forest (quadrat 9, fig. 44). The manner of invasion of the sedge mat by the sphagnum is shown. To avoid confusion the distribution of the bog shrubs is indicated only in a general way. The trees of the various species, their locations, and ages are given in the manner made use



FIG. 43.—*Sphagnum-Ledum* society invading the upland forest: the view is taken from the bog, and shows the bog vegetation climbing the slope to a height of 4.5 m.; Raspberry Island.

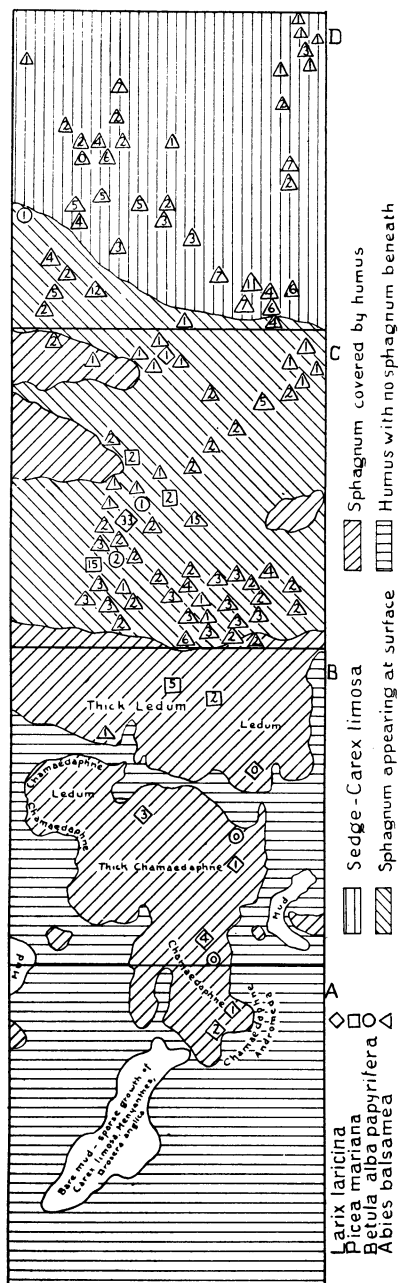


FIG. 44.—Quadrat 9: Raspberry Island; for explanation of symbols see fig. 6

of in the charts of the climax forest.

The most important fact to be obtained from the diagram is that in no part of the section is there anything approaching pure bog forest. In quadrats *A* and *B* there is a mere scattering of invaders; *C* and *D* are occupied by a young climax forest growth with a few bog trees, most of which are relicts. The absence of pure bog forest is due to the fact that the trees of the climax stage follow immediately after the first invading bog trees, or even accompany them. In accordance with the usual habit of the species, balsam seedlings germinate in enormous numbers, and although many of them succumb to the stress of competition, they shade the ground so that no more bog trees, which are light-requiring species, can start. The climax trees, *Abies*, *Betula*, and *Picea canadensis*, having come into possession are able to hold their ground in the manner described in an earlier section of this paper. The further history merely records the gradual dying out of the bog relicts.

Though there is little *pure* bog forest upon Isle Royale, there is abundance of a very characteristic type which may be called "impure" bog forest; that is, forest composed of a mixture of bog and climax trees. Upon Raspberry Island it is poorly developed,

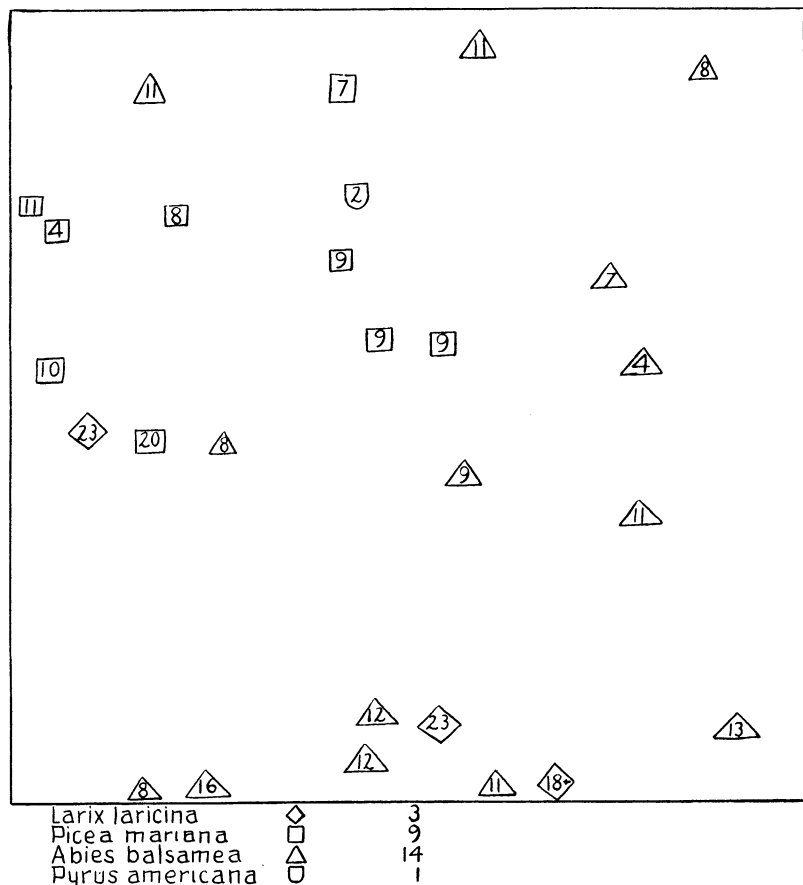


FIG. 45.—Quadrat 10: bog near Park Place Hotel; for explanation of symbols see fig. 6.

but there is an excellent sample near the Park Place Hotel on Rock Harbor (Sec. 3, T. 66 N., R. 33 W.). A quadrat in this locality was studied and the results are shown in fig. 45. The oldest trees here were the three tamaracks, and they were also much the largest, being 2.75–5.25 dm. thick, and towering above their companions.

One of them was hollow, and all were more or less attacked by rot. The black spruces were found to be somewhat younger than the tamaracks. All were solid to the heart. The balsams, which were most numerous of the tree species, were of various ages from 47 to 161 years. No young balsams were present and the average age

was very high (105 years). All showed signs of suppression during early life, probably due to shading by the faster growing bog trees. Within the last half-century the tops have reached the sunlight, and most of the balsams are now growing rapidly, though many are rotten hearted, as is common with this species. Two birches close to the quadrat, 1.5 dm. and 2.25 dm. in diameter, were found to be 62 and 69 years old respectively. No white spruce occurred in this locality, but the species is present in most areas of bog forest. A striking fact is the absence of reproduction (fig. 46). No tree younger than 47 years was seen except a few one or two-year-old seedlings of birch and mountain ash, which seem able to germinate in deep shade but not to continue growth.



FIG. 46.—Bog forest interior; locality of quadrat 10: two large tamaracks in the background; black spruce, balsam, and *Alnus incana*; carpet of *Carex trisperma* with *Petasites* and other species; note absence of tree reproduction.

The history of the area is probably as follows. The present generation of trees of both bog and climax type started during the period of open bog conditions, and growing up together produced so dense a shade as to inhibit the starting of new growth beneath them. Shelter from wind, due to the depression in which they grow, is doubtless the reason for the absence of windfalls and the unusually long life of the balsams. No reproduction will take

place until light is admitted to the forest floor by the destruction of some of the present generation.

The characteristic bog forest shrubs are the alders. *Alnus incana* is found principally near the bogward edge, while *Alnus crispa*, belonging rather to the climax forest, inhabits the landward portions.

In the lower vegetation mosses are most prominent both in quantity and variety; 22 species were taken from a single area of bog forest. *Sphagnum* spp. (relicts of the open bog stage), *Calliergon Schreberi* (Willd.) Grout, and *Hylocomium proliferum* (L.) Lindb. make up the bulk of the moss carpet. Sharing the forest floor with these is *Carex trisperma* Dewey which, accompanied by *C. leptalea* Wahlenb. and *C. tenella* Schkuhr, forms dense green mats of considerable size. In some places *Lycopodium annotinum* L. covers the ground, and in others there is a rank growth of *Equisetum sylvaticum* L. As minor features there are certain herbs that particularly characterize the bog forest. The most numerous are *Habenaria obtusata* (Pursh) Richards, *Listera cordata* (L.) R. Br., *Smilacina trifolia* (L.) Desf., *Phegopteris Dryopteris* (L.) Fée, *Mitella nuda* L., *Coptis trifolia* (L.) Salisb., *Viola incognita* Brainerd, *Petasites palmatus* (Ait.) Gray.

The outstanding feature in the later part of the bog succession is the telescoping of stages. The sphagnum-shrub stage (when present) is hardly well established before the bog trees enter, and immediately following them or often actually with them come the climax trees. The reason for the early establishment of the latter is found in the likeness between the bog soils and those of the forested uplands. Those of the uplands are nearly as peaty in texture and properties as are those of the bogs. The causes of the peatiness of the upland soils trace back to other factors: low evaporation rate due to low temperatures; poor drainage because of solid rock substratum; and probable paucity of certain types of bacterial and fungal life. It follows, the two soils being much alike, that whatever trees can grow upon one may exist also upon the other.

5. Two types of bogs

One of the numerous questions that could not be settled with entire satisfaction related to two fairly distinct types of bogs

involving somewhat different courses of succession. One had an abundant growth of sphagnum associated with much *Ledum*, and *Picea mariana* and *Larix* composing the bog forest. Those of the other type had little sphagnum, often practically none, and in these *Ledum* was rare or absent and *Picea mariana* almost never found, the bog trees being *Larix* and *Thuja* or *Larix* alone. The Raspberry Island bog is an excellent example of the first, which we may designate the sphagnum type; and Sucker Lake and the other pond near Tobin's Harbor illustrate the second, or sedge type. In some cases these types may represent stages in the same succession, since sphagnum often does not become dominant until late in the history of a bog, and *Ledum* and *Picea mariana* follow the sphagnum, being dependent upon its presence. But it is certain that in many cases the *Sphagnum-Ledum* stage is entirely eliminated, and that when this happens *Picea mariana* does not appear, or holds a very subordinate place in the bog forest. The succession in such cases is as follows: (1) aquatics, (2) sedge mat, (3) shrub zone (*Chamaedaphne*, *Andromeda*, *Alnus incana*), (4) bog forest (*Larix*, often with *Thuja*). It is obvious that *Sphagnum* is the critical plant, since *Ledum* and *Picea mariana* come later and only in bogs where the moss is abundant.

Certain differences were noted in the conditions prevailing in the two types of bogs. It was universally true in the sphagnum bogs that were visited that the drainage was poor or lacking, the only water loss being due to very slow seepage and evaporation. Those of the sedge type on the contrary were usually well drained. There was often open water in the center, in which case the bog might well be at a stage earlier than that of sphagnum dominance. The covered bogs without much sphagnum usually possessed one or more small streams flowing in and an active outlet. In a few cases, however, the drainage was seemingly as poor as in the sphagnum bogs. As to the way in which these drainage differences affect the vegetation, if they do affect it, nothing was determined.

Another fact was noted which quite certainly has a bearing upon the presence or absence of sphagnum. It was found that the sedge mat is composed of different species in the two types of bogs. In the sphagnum bogs *Carex limosa*, a low, soft, loosely growing

stoloniferous species, was usually the principal mat-former, and *Menyanthes*, with somewhat similar characteristics, was next in importance (compare figs. 33 and 38). In those of the sedge type, tall stiff sedges growing in dense clumps were most important, forming a thick meadow-like growth. *Carex filiformis* was the commonest species, but certain areas were found to be dominated by *Scirpus caespitosus* L., the most densely tufted of all the sedges. These two kinds of sedge mat form very different substrata for the growth of the sphagnum. On account of the shortness and softness of *Carex limosa* the moss is never seriously shaded where that sedge is dominant, and it is able to grow over and around the *Carex* and *Menyanthes* plants and thus to spread laterally with ease. The sedges in this case offer no effective resistance, and the sphagnum soon gains the ascendancy over them. Where *Carex filiformis* and plants of similar habit are the principal mat-formers the moss, if it starts among the closely placed clumps, is shaded from the beginning. It cannot spread laterally among the dense clusters of thick culms, and so remains in a half-smothered condition until exterminated through the advance of the shrubs and trees. The distribution of the two kinds of mat-forming plants still remains to be accounted for, and for this I have as yet no explanation. It is entirely possible that the type of sedge which gains the dominant place in a given bog may be determined merely by accidental causes.



FIG. 47.—Bog forest in well drained portion of a bog near Siskowit Lake: *Larix* and *Alnus incana*.

Occasionally the two phases may be seen in a single bog. For

instance, in a locality near Siskowit Lake (Sec. 32, T. 65 N., R. 35 W.) the central area (which is better drained than the rest, having a sluggish stream meandering through it) is of the sedge type. Some patches of bog forest near the stream are made up almost entirely of *Larix*, with much *Alnus incana* as undergrowth. In the poorly drained areas near the margin the forest is pure *Picea mariana*, and the ground is carpeted with solid sphagnum covered with an abundant growth of *Ledum*. These two phases are shown in figs. 47 and 48.



FIG. 48.—Bog forest in poorly drained area; same locality as fig. 47; *Picea mariana*, *Ledum*, and *Sphagnum*.

The delta swamp succession

I. Extent and distribution

The delta swamp succession comprises the successive stages of vegetational development which culminate in the establishment of the climax forest upon the deltas and alluvial plains of the streams. These societies do not occupy an extensive area in the aggregate, but they are exceedingly interesting because of the close interdependence between the successional and the physiographic processes. Delta swamps of various sizes are found at the heads of most of the bays,

and are probably present also where streams of any size enter the larger lakes. Protection from the waves and currents of Lake Superior is naturally essential to their development. The localities studied were as follows: head of McCargoe's Cove (Sec. 26, T. 66 N., R. 35 W.), Brady Cove (Sec. 18, T. 66 N., R. 35 W.), Duncan Bay (Sec. 6, T. 66 N., R. 33 W.), Lake Richie outlet at Chippewa Harbor (Sec. 18, T. 65 N., R. 34 W.), Hay Bay (Sec.

24, T. 64 N., R. 37 W.), head of Siskowit Bay (Sec. 33, T. 64 N., R. 37 W.).

II. Physiographic development of the habitat

The history of the present deltas began with the initiation of stream activity as the island emerged from the lake. The amount of erosion accomplished by the streams of Isle Royale has been very slight. The sources of the materials transported by them have been principally two: the products of wave erosion left high and dry as the lake level sank, and weathered rock material, including some decomposed by organic agencies. Deposits were made at the mouths of the streams at all stages during the emergence of the island. As the lake surface sank these were transported to successively lower levels, and more materials were added. Of course some of the earlier deposits may have been so situated as to have escaped removal, but no such remnants have been reported. It is therefore probable that the present deltas include most of the materials that made up the earlier ones, brought down from level to level as the streams were repeatedly rejuvenated by successive sinkings of the lake surface.

Delta building seems to have practically ceased, at least temporarily, for three reasons: (1) the available loose material accumulated during the successive stages has all been brought down and deposited; (2) the complete forest covering of the uplands practically inhibits further weathering and erosion, except what may be accomplished by the slow organic processes; (3) (applicable only to northeastward-flowing streams, which, however, are in the majority) tilting has taken place in the Lake Superior region since the formation of the Nipissing beach (ADAMS 4). At Isle Royale the elevation of this beach is about 18 m., and it rises northward to 27 m. at Nipigon. This has decreased the gradient of northeastward-flowing streams and thus has tended to reduce their erosive and transporting power.

The result of these processes has been the formation of flat delta plains of gravel, sand, and silt at the heads of many of the harbors, with streams, practically currentless, meandering over them. Cut-and-fill and scour-and-fill are going on to some extent

in these streams, which processes are due principally to alternating currents produced by seiche movements (ADAMS 4) of the waters of Lake Superior. The currents thus produced are quite considerable. At one moment there is a strong outward flow; a few minutes later the movement may be just as swift in the opposite direction. The effect of the seiche current is practically the same as that of an ordinary stream current. It undermines the bank in some places and deposits the eroded materials in others. On account of its alternating direction the gradational effects in a particular case cannot be so simply worked out, but judging from the relative positions of the eroding and depositing portions of the banks it seems probable, as one would naturally expect, that the outward current is the more effective. It is possible that occasional heavy rains may considerably increase the volume and velocity of the streams. The channels are not ordinarily sunk far into the sedimentary substratum. Their banks appear largely as vertical sections of the layer of plant growth which has spread over the delta plain.

III. Vegetational development in the habitat

The first vegetation upon the delta deposits enters when the water over them shallows sufficiently to permit the growth of aquatics of the pondweed type. Next come water lilies and rushes, and when the sediments accumulate until they reach nearly to the surface, sedges gain a foothold and soon form a mat. Up to this point the development has followed the same course as the bog succession. Important differences now appear. The sedge mat does not build out over the water, probably because of wave and ice action, since the bodies of water into which the streams flow are rather large and open. The sedge mat stage does not last long, but is very soon superseded by a dense growth of tall grasses, among which *Calamagrostis canadensis* (Michx.) Beauv. is by far the most important. It is this type of plant, growing in dense, closely placed stools, that forms the bulk of the stratum of plant remains which finally covers the plain. The grasses are followed by shrubs, and these by the swamp trees, which finally give way to the climax forest.

Among the delta swamps studied, the largest was at the head of McCargoe's Cove. The alluvial flat was here 0.8 km. long by 0.4 km. wide. All the stages are here well developed except the swamp forest, which has been fire-swept. Part of the meadow-like marsh is shown in fig. 49, and a sketch map of the delta is given in fig. 50. Farthest out, in water a meter and more deep, is a zone of *Potamogeton perfoliatus* L. Within this, in a few inches of water, grows *Equisetum fluviatile* L. Next comes the sedge mat, firmly grounded, with *Carex filiformis* as the principal species, accompanied



FIG. 49.—Delta swamp at the head of McCargoe's Cove: sedge, grass, and shrub societies are shown; the swamp forest has been burned.

by bog herbs. The area dominated by *Calamagrostis* is the most extensive, and its level is perceptibly higher than that of the sedge zone. With *Calamagrostis* grow other herbaceous species, many of them tall, such as *Thalictrum dasycarpum* Fisch. and Lall. (tall meadow rue), *Chelone glabra* L. (turtle-head), *Epilobium angustifolium* L. (fireweed), and *Symplocarpus foetidus* (L.) Nutt. (skunk cabbage). Stools and patches of *Calamagrostis* were seen as invaders of the sedge society, and occasional shrubs, pioneers of the next group, were scattered over the area occupied by the grass.

Myrica Gale L. (sweet gale) is the first shrub to invade the

meadow swamp. It is followed by *Alnus incana*, which at first is pure, but farther back is found mixed with other shrubs: *Cornus stolonifera* Michx. (red osier dogwood) and *Viburnum pauciflorum* Raf. (high bush cranberry). With these come the invaders from the forest, *Fraxinus nigra* Marsh (black ash) being usually the first arrival. Burned stumps indicate that there was once an extensive

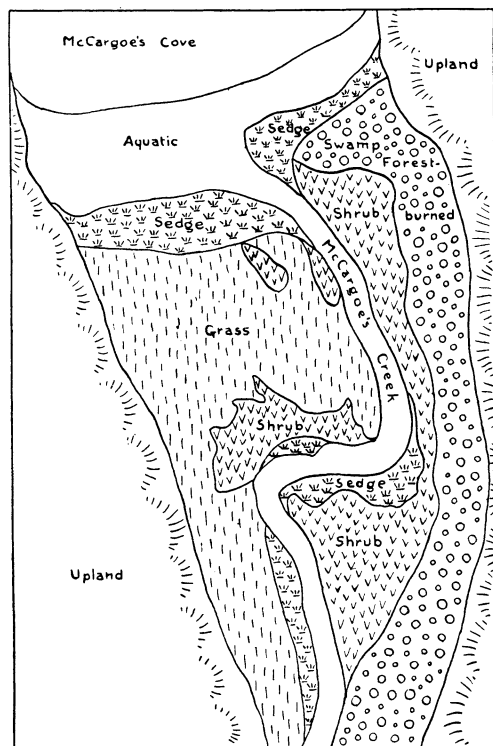


FIG. 50.—Sketch map of the delta at the head of McCargoe's Cove.

development of swamp forest along the east side of the delta, in which *Thuja* was the important tree.

The stream which winds through the swamp is 6–10 m. wide and 0.3–1 m. deep. Its channel is constantly changing by reason of its own undermining and depositional activity. Near the outer edge of the marsh it crosses the belt of sedges. Farther back it is bordered by various societies. Where it cuts into the grass-covered areas erosion by undermining is going on, and a section of peat sometimes 0.6 m. in height is exposed. For

considerable distances shrubs are also being undermined, and at one point the stream in its meandering has invaded the area of former swamp forest and has caused the overthrow of many trees. The material eroded from the banks is deposited where the current slackens, and in such places the normal succession of plant stages is in progress; aquatics first, followed by a sedge mat when the

deposit reaches the surface. Frequently the first invaders are stools of sedge or rootstocks of *Nymphaea* and *Calla* which have been washed out from some eroding portion of the shore.

It may thus be seen how the plant life supplements the physiographic processes. Upon one bank the current may be steadily destroying the vegetation (grasses, shrubs, and even trees); while on the other, where deposition is in progress, the same types are being developed through the normal course of the swamp succession.

Note should be made of the peculiarly rich aquatic flora which inhabits the shallows of this and similar sluggish streams. The list of species obtained in the several localities of this type includes the following of special interest: *Nymphaea advena* Ait., *Vallisneria spiralis* L., *Utricularia vulgaris* L. var. *americana* Gray, *U. intermedia* Hayne, *U. minor* L., *Myriophyllum verticillatum* L. var. *pectinatum* Wallr., *M. spicatum* L., *M. alterniflorum* DC, *Potamogeton natans* L., *P. alpinus* Balbis, *P. amplifolius* Tuckerm., *P. heterophyllus* Schreb., *P. heterophyllus* f. *terrestris* Schlecht., *P. praelongus* Wulf., *P. perfoliatus* L., *P. zosterifolius* Schumacher, *P. obtusifolius* Mertens and Koch, *P. filiformis* Pers., *Callitriche palustris* L., *Castalia tetragona* (Georgi) Lawson, *Bidens Beckii* Torr., *Scirpus subterminalis* Torr., *Sparganium diversifolium* Graebner, *S. minimum* Fries, *Sagittaria latifolia* Willd. f. *hastata* (Pursh) Robinson, *S. cuneata* Sheldon, *Lemna trisulca* L., *Ceratophyllum demersum* L., *Hippuris vulgaris* L., *Glyceria borealis* (Nash) Batchelder, *Calla palustris* L., *Isoetes macrospora* Dur. Though not a plant, *Spongilla* should be mentioned as an important element in the aquatic life.

At the head of Duncan Bay there are two delta swamps, both smaller than the one just described. One of these was studied with care, and the locality is included here because the swamp forest is well developed. *Fraxinus nigra* is the pioneer, and is present, but not abundant, in the mature forest. *Thuja* comes next and is the most important species. *Larix*, *Picea canadensis*, *Abies*, and *Betula alba* var. *papyrifera*, in order of abundance as named, complete the list. In passing toward the shoreward edge of the swamp forest *Larix* is the first to disappear. *Thuja* holds out much longer, and the ground is covered in places with tangles of layered branches

from it. The young trees are largely balsams. The herbaceous growth is practically the same that is found in the bog forest. It will be noted that all the trees of the climax forest are present here, and that the stages are telescoped as in the bog succession.

A locality where the climax condition had been almost attained was found in a narrow stream valley at the head of Brady Cove (Sec. 18, T. 66. N., R. 35 W.). The forest here, which fills the valley, is of the climax type except for an occasional ancient *Thuja* and a slight admixture of *Fraxinus nigra*. Fallen trunks of *Thuja* are fairly numerous. The shrubs and herbs are a mixture of swamp forest and climax forest species.

That there is a general resemblance between the bog succession and the delta swamp succession is very evident. There are also some striking differences which are constant in the localities studied. Most important of these are the following: sedge mat not floating; interpolation of grass stage as the most important peat-forming agency; absence of sphagnum, true bog shrubs, and *Picea mariana*; dominance of *Thuja* in the swamp forest.

It is conceivable that under certain circumstances one succession might pass over into the other. This seems to have happened at the head of Siskowit Bay just north of Senter Point. A large swampy area has been cut off from the bay by a high curving beach ridge 1 km. long. That there was originally a delta swamp here is shown by the presence of a remnant of the former stream, a winding strip of water ending abruptly against the outer ridge. For some reason, possibly on account of post-Nipissing tilting, the current of the stream became insufficient to keep its outlet open in opposition to the vigorous wave action upon the shore of the bay. The resulting stagnancy has brought about a partial change to bog conditions. The former stream is partly filled with an open growth of *Menyanthes*, *Equisetum fluviatile*, *Utricularia intermedia*, and *Potamogeton heterophyllus*. Along the water's edge there is a band of nearly pure *Carex filiformis*, recently established. The body of the swamp is occupied by a sedge-grass society, in which *Scirpus caespitosus* is dominant. Accompanying species are *Carex exilis* Dewey, *Muhlenbergia racemosa* (Michx.) BSP, *Sarracenia purpurea* L., *Vaccinium Oxycoccos* L., *Aster umbellatus* Mill. var. *pubens*

Gray, *Solidago uliginosa* Nutt. Shrubs are scattered over the whole area, the principal species being *Potentilla fruticosa* L. and *Myrica Gale* L. The bog forest is of considerable extent and the trees are *Thuja*, *Larix*, and *Picea mariana*. Near the forest edge there is considerable sphagnum in hummocks much overgrown with grasses and other plants. The composite character of the vegetation in this locality is plain. It is certain that the change from swamp to bog conditions has been very gradual, and it is possible also that there has always existed here a slight element of bog vegetation.

THE SECONDARY SUCCESSION

The burn succession

I. Causes and extent of fires upon Isle Royale

During the period of mining activity upon Isle Royale fires were of frequent occurrence and many square kilometers were swept by them. Since the abandonment of the mines they have been much less frequent, so that most of the burned areas found today have already gone through a considerable period of forestward development. There is evidence that fires occurred long before the appearance of white men. A layer of burned wood deeply buried was found in the humus upon Smithwick Island, where otherwise absolutely no sign of burning was to be seen. Such fires must have been started either by Indians or by lightning. It is nearly certain that fire has played a part in the vegetational history of almost all if not the entire forested area of the island.

II. Effect of fire upon the climax forest

The effect of the destruction wrought by a forest fire is essentially to bring about a return to a more or less xerophytic condition, which is followed by a readvance leading again to the climax forest. The secondary development may be along the line of the original primary succession, but factors are usually present which bring about pronounced modifications in the process. Obviously the burn succession is exceedingly variable, and cannot be described in terms that will even approximately fit every case. The variable factor that is most important in creating differences in the succession is the severity of the fire. In respect to this two cases may be roughly distinguished.

1. *Humus little harmed*.—This is the commonest type of burn upon Isle Royale and results in the development of a characteristic “burn forest” preceding the reestablishment of the climax. The composition of such a forest is mainly the outcome of the differing success with which the various species withstand the effects of the



FIG. 51.—Recently burned area on Smithwick Island: fireweeds dominant; a relict birch at the left; unburned forest in the background.



FIG. 52.—Young birch stump sprouts in a two-year-old burn near Siskowit Lake.

fire. The coniferous element of the climax forest, consisting of *Abies balsamea* and *Picea canadensis*, is entirely eliminated by a fire of any severity. *Betula alba* var. *papyrifera*, on account of its dry papery bark, is very inflammable, and the aerial portions are quickly destroyed. The underground parts, however, are not killed as are those of the conifers. They persist with great tenacity through most unfavorable conditions, provided the humus in which

they are buried is unharmed, and are the most important contributors to the forest which immediately begins its development. *Pyrus americana* is similar to the birch in this respect, but is much less abundant. The shrubs of the climax forest seldom survive, though occasionally in a moist hollow a clump of *Taxus* will persist. The plants of the forest undergrowth, being close to the damp ground, frequently live through the fire. Some of them quickly succumb to the hard conditions which ensue, but certain species seem to thrive better than ever after the destruction of the forest cover. Prominent among the latter class are *Cornus canadensis*, *Linnaea borealis* var. *americana*, and *Maianthemum canadense*. These, which usually grow rather sparsely in the shade of the climax trees, come to cover large areas, flowering and fruiting luxuriantly. The first is one of the most characteristic species in the undergrowth of the burn forest.

Upon areas where the forest has been destroyed but the humus little harmed the progress of the burn succession is commonly as follows. During the first growing season after the fire those relicts which have survived renew their growth, and many new arrivals appear. Certain of the latter are much the most prominent features for a number of years. These are the familiar fireweeds, *Epilobium angustifolium* L. and *Anaphalis margaritacea* (L.) B. & H. (fig. 51).

Although the fireweeds give tone to the landscape for the first few years, the trees of the future forest begin their development equally early. The birches of the original stand, whose subterranean parts are still alive, sprout luxuriantly from the stump (figs. 52, 53). Often a ring of a dozen or more shoots appears where a single birch of the previous generation stood. Many of these die, but some develop into trees. Seedling birches and aspens (*Populus tremuloides*) add to the number, but upon Isle Royale the birch sprouts greatly predominate. The result is the development of a forest composed mainly of even-aged birches in clumps of 2-6 or more (fig. 54). A rich shrubby vegetation accompanies the trees. *Rubus idaeus* var. *aculeatissimus* is usually the first. *Diervilla* *Lonicera* Mill, *Corylus rostrata* Ait., and *Rubus parviflorus* Nutt. follow. When the birches have attained a size sufficient to produce

moderate shade, the last named shrub (white-flowered raspberry) often forms a dense tall thicket growth beneath them. There is also a characteristic group of herbs that follow close upon the decline of the fireweeds. These are *Castilleja pallida* (L.) Spreng. var. *septentrionalis* (Lindl.) Gray, *Lilium philadelphicum* L., *Pteris aquilina* L., and others in the early stages; and *Aster macrophyllus* L., very abundant in the mature burn forest. A forest mainly of birches in clumps, with undergrowth as described above, is practically certain indication that fire has recently visited the area.



FIG. 53.—A group of birch stump sprouts in an area that was burned about 35 years ago: the original trunk is shown; near Park Place Hotel.

Frequently neighboring burns of different ages are indicated by patches of birch forest of differing height.

None of the areas of burn forest of historic age upon Isle Royale are old enough to show the late stages in the transition to the climax. The process is indicated, however, by the frequent occurrence of young spruce and balsam under the light shade of the birches. Occasional conifers germinate immediately after the fire, but the thorough occupation of the ground by the fireweeds and the rapid growth of the birch sprouts, as well as the dryness of the ground, prevent them from starting in abundance. The devel-

opment of the burn forest is exceedingly rapid, thanks to the prolific sprouting of the birch, but the transition from burn forest to climax seems to be a slower process. Occasional areas of climax forest in which the birch element is mainly composed of groups of immense stump sprouts probably represent the penultimate stage in a burn succession following some prehistoric fire.

The effect of fire upon the composition of the flora is shown in table VI. The statistics were obtained from a study of areas of equal size in the unburned and burned portions of Smithwick



FIG. 54.—A young burned forest composed mainly of birches in clumps: the lower growth is *Juniperus communis* var. *depressa*, *Pteris aquilina*, and other species; near Park Place Hotel.

Island. The fire occurred about 15 years ago. The points to be noted are the destruction of the conifers and a part of the herbaceous flora, the increase of *Betula* and another portion of the herbaceous vegetation, and the appearance of *Populus*, *Rubus*, and the fireweeds.

2. *Humus destroyed; bare rock exposed*.—In such cases the reestablishment of the climax follows closely along the line of the rock shore succession, through lichen and crevice plant, and heath mat stages. Such differences as occur are due to the more thorough disintegration of the rock with greater abundance of soil materials

resulting therefrom; the presence of more or less humus at the beginning (it rarely happens that fire destroys every vestige of organic matter, and even a very small quantity in a rock crevice is of great assistance in hastening the establishment of vegetation); frequent protection from the drying and mechanical effects of wind;

TABLE VI

| Species | Climax forest | Burn |
|--|---------------|---------------|
| <i>Abies balsamea</i> | 65 | I |
| <i>Betula alba</i> var. <i>papyrifera</i> | 6 | 117 (sprouts) |
| <i>Picea canadensis</i> | I | ... |
| <i>Pyrus americana</i> | 13 | ... |
| <i>Populus tremuloides</i> | .. | 16 |
| <i>Taxus canadensis</i> | 14 | ... |
| <i>Viburnum pauciflorum</i> | I | I |
| <i>Rubus idaeus</i> var. <i>aculeatissimus</i> | .. | 74 |
| <i>Aralia nudicaulis</i> | 21 | ... |
| <i>Mitella nuda</i> | 21 | ... |
| <i>Trientalis americana</i> | 13 | ... |
| <i>Linnaea borealis</i> var. <i>americana</i> | 6 | 30 |
| <i>Clintonia borealis</i> | 2 | ... |
| <i>Epilobium angustifolium</i> | .. | 806 |
| <i>Anaphalis margaritacea</i> | .. | 421 |
| <i>Maianthemum canadense</i> | * | 312 |
| <i>Calamagrostis canadensis</i> | .. | 83 |

* Frequent in most parts of climax forest.

presence of a large body of invaders ready to advance from all directions. All these modifying influences tend to hasten the progress of the succession. Areas where fire has exposed the bare rock are found principally upon the tops of ridges, since the soil in such places is usually both shallow and dry, and whatever remains after the fire is washed away to lower levels.

III. Effect of fire upon the xerophytic and bog forests

When the jack pine-black spruce forest is burned, much of the humus is apt to be destroyed also, as the soil is commonly thin and dry. A few observations indicate that this type often succeeds itself. The pine grows faster and so for a number of years is the dominant tree. In one burned locality was found an open growth of pines 4-7 m. high, even-aged, averaging 28 years. Beneath

them were scattered black spruces, few more than 1 m. high, also even-aged, and averaging more than a year older than the pines.

In extensive fires the patches of bog forest occupying the depressions often escape entirely because of abundant moisture. When they are burned over the coniferous element is destroyed, and the birches if present sprout from the stump. The underground portions of the two species of *Alnus* survive and renew growth, and the result is frequently a dense alder-birch thicket, which probably passes directly into the climax type. When the scattered trees growing upon an open bog are killed by fire the sphagnum, being usually saturated with water, seldom suffers severely. New bog trees begin growth and the succession goes on as before.

SUMMARY.—THE SUCCESSIONS

Primary successions

The xerarch successions

Every part of Isle Royale has at some point of its subaerial history been shore.

The present coast of the island is made up of rock shores and beaches, the former being much the more extensive. Each type possesses its characteristic series of successional stages, the ROCK SHORE SUCCESSION and the BEACH SUCCESSION, both resulting finally in the establishment of the climax forest.

With regard to area vegetated through its instrumentality, the rock shore succession is by far the most important of all the successions of Isle Royale.

The full series of the rock shore succession includes in its early stages three subsuccessions which later unite into a single series.

The *rock surface subsuccession* advances through crustose lichen and foliose lichen stages to a condition in which the large cladonias are the most important element. The process of invasion along this line alone is very slow.

The pioneers of the *crevice subsuccession* are certain herbs, notably *Potentilla tridentata*, whose principal rôle is the formation of humus. Trailing shrubs succeed them, the most important being *Juniperus horizontalis*, *J. communis* var. *depressa*, and *Arctostaphylos Uva-ursi*. These spread over the rocks from the

crevices in all directions, and weaving among the cladonias and plants of the rock pools bring about the formation of a firm mat. The crevice vegetation is of extreme importance because of its rapidity of development and its preeminent part in the formation of the heath mat. Forest establishment is accomplished much sooner where crevices are abundant in the rock than where they are scarce.

The *rock pool subsuccession* goes through its development in depressions where water stands at least a part of the time. These become gradually filled after the manner of the bog succession, and the vegetation later becomes an element in the formation of the heath mat.

The *heath mat* results from the coalescence of the vegetation developed through the instrumentality of the three subsuccessions named above.

The *climax forest* often follows immediately after the formation of the heath mat, the trees obtaining their first foothold in the crevices. A relatively xerophytic forest stage characterized by *Pinus Banksiana* and *Picea mariana* sometimes intervenes, in which *Pinus* is the pioneer and *Picea* remains for some time after the climax trees have attained dominance.

Telescoping of stages is pronounced throughout the series, so that pioneer and climax forms, with those of all intermediate stages, are frequently found occupying a single limited area.

The effect of special conditions upon the rock shore succession is expressed in the two following laws:

1. The lower limit of possible forest extension is determined approximately by the upper limit of effective wave and ice work, the lake level remaining constant.

2. The extent to which the forestable territory has been occupied at the present day depends upon the rapidity of invasion, which is governed by the character of the rock, the angle of slope, and the degree of exposure to winds.

The operation of these laws results in the production of three phases of rock shore vegetation, characterized respectively by (A) climax forest to the water's edge, (B) a zone of incomplete invasion, (C) abrupt transition from bare rock shore to climax forest.

During the early subaerial history of Isle Royale the rock shore succession may have differed from that of the present day. A study of Gull Islands indicates that birds may have been important agents in determining the composition of the primitive rock shore flora of the island.

The beaches on account of their sheltered location usually bear the climax forest down to its limit of possible extension. Low shrubs of various kinds are the most important pioneers in the beach succession, and larger ones, especially *Alnus crispa*, intervene before the establishment of the climax type.

The hydrarch successions

The bog succession

Physiographic development.—The depressions which now contain lakes or bogs owe their origin to glacial modification of the preglacial topography; sometimes to the cutting off of bays or channels by wave-built bars.

The physiographic history of the habitat in which the bog succession runs its course comprises two stages: the channel-bay stage and the lake stage. The lakes and harbors are tending toward extinction through the agencies of down-cutting of outlets, sedimentation, and vegetation, of which the last is the only one of importance at the present time. The lake stage ends when vegetation, aided by the other agencies, has entirely eliminated the open water.

Vegetational development.—During the channel-bay stage aquatics first appear and gradually increase with increasing shelter; the beginnings of the sedge mat are occasionally present.

During the physiographic lake stage all the vegetational stages of the succession appear in order: aquatics (usually already present), sedge mat, sphagnum-shrub, bog forest. All may have their beginnings at practically the same time. The sedge mat is usually the most prominent feature at this period. The sedges gain their first foothold in shallow water close to shore and build a floating mat out over the water. They are by far the most important agents in peat formation.

During the covered bog stage the plant societies are successively eliminated by the centripetal encroachment of the various zones.

Two lines of succession are distinguished after the sedge mat stage. One is characterized by *Chamaedaphne*, *Andromeda*, and *Alnus incana* in the shrub stage, practical absence of sphagnum, and by *Larix* and sometimes *Thuja* in the bog forest; the other by *Chamaedaphne* and *Andromeda* followed by *Ledum* in the shrub stage, abundance of sphagnum accompanying the shrubs, and by *Larix* and *Picea mariana* in the bog forest. Sphagnum is the critical plant in the differentiation of the two series, since *Ledum* and *Picea mariana* appear later, and only in cases where sphagnum is abundant. The differences may be related to differences in drainage, since those bogs containing little sphagnum are usually well drained, while in those with abundance of sphagnum, as far as observation has gone, drainage was very poor or lacking entirely. A contributing factor is found in differences in the composition of the sedge mat preceding the shrubs and sphagnum. In the sphagnum bogs *Carex limosa* is the principal mat-forming species. Being low and soft, it offers no resistance to the spread of the moss. In the bogs with little sphagnum *Carex filiformis* is the important mat-former. On account of its height and stiffness and dense growth it produces unfavorable conditions for the spread of sphagnum. The reason for the differing distribution of the two carices is unknown; it may be merely accidental.

The sphagnum is a superficial layer supported upon the sedge mat, and contributes little toward peat formation. It begins growth some distance within the bog margin and spreads both ways, slowly toward the margin, faster centerward. The area between the sphagnum and the upland commonly forms a marginal trench. In some places the moss by recent invasion has obliterated the marginal trench, and occasionally it transgresses the bog margin, spreading up the forest floor for several meters.

The sphagnum spreads marginally, surrounding and smothering such plants as cannot keep pace with its growth. Certain species by upward elongation are able to survive for some time, especially *Andromeda* and *Chamaedaphne*, the latter persisting longest.

Ledum almost invariably follows the sphagnum, and its root system is usually strictly confined to the masses of it. It forms a

very dense growth, and through its shading power and the great amount of waste that falls from it finally eliminates the lower shrubs and stops the upward growth of the moss.

The bog trees, *Larix*, *Thuja*, *Picea mariana*, usually follow the sphagnum when it is present. When it is lacking they start upon the sedge mat with the shrubs. The climax trees enter very soon after or often actually with the bog trees, so that pure bog forest is practically absent. The bog trees die out because they are intolerant of shading, and the climax forest results.

Telescoping of stages is prominent throughout the late history of the succession.

The reason for the early establishment of the climax forest is found in the likeness between the bog soils and those of the forested uplands, the latter being almost as peaty as those of the bogs. It follows that whatever trees can grow upon one soil may also exist upon the other.

The delta swamp succession

Delta deposits are found in most of the sheltered bays where streams enter from the upland.

The succession of vegetation upon these deposits passes through the following stages: (1) aquatics; (2) sedges; (3) grasses (*Calamagrostis canadensis* most important), which form broad meadow-like growths and produce a limited amount of peat; (4) shrubs, among which *Myrica Gale* and *Alnus incana* are most important; (5) swamp forest, made up of *Thuja occidentalis*, *Larix laricina*, and *Fraxinus nigra*, the first being dominant; (6) climax forest of *Abies balsamea*, *Betula alba* var. *papyrifera*, and *Picea canadensis*.

There is a general likeness to the bog succession; among other points, in the early establishment of the climax forest after the coming in of the swamp trees.

The important points of difference from the bog succession are: the firmly grounded sedge mat; interpolation of the grass stage; absence of sphagnum, bog shrubs, and *Picea mariana*; dominance of *Thuja* in the swamp forest.

Intermediate conditions between the two successions occur, and actual transition from delta swamp to bog succession occasionally takes place.

LITERATURE CITED

1. ADAMS, C. C., Postglacial origin and migrations of the life of the north-eastern United States. Jour. Geog. 1: no. 7. 1902.
2. ———, The postglacial dispersal of the North American biota. Biol. Bull. 9: 53-71. 1905.
3. ———, An ecological survey in northern Michigan. A report from the University Museum, University of Michigan, published by the State Board of Geol. Surv. as part of report for 1905. Lansing, Mich. 1906. Pp. 48-55 and 86-92, written by Dr. A. G. RUTHVEN, deal with the plant ecology of Isle Royale. 1906.
4. ———, An ecological survey of Isle Royale, Lake Superior. A report from the University of Michigan Museum, published by the State Biol. Surv. as a part of Rep. Geol. Surv. 1908. Lansing, Mich. 1909. Contains the following sections dealing directly or indirectly with the plant ecology: Isle Royale as a biotic environment, pp. 1-53, by C. C. ADAMS; The ecological relations of the invertebrate fauna of Isle Royale, Mich., pp. 57-78, by H. A. GLEASON; Notes on the vegetation of Isle Royale, Michigan, and annotated list of plants, pp. 217-248, by W. P. HOLT.
5. ATKINSON, G. F., College Botany. New York. 1908.
6. AYRES, H. B., Timber conditions of the pine region of Minnesota. U.S. Geol. Surv. 21st Ann. Rep., Pt. V. 673-689. 1900.
7. BELL, ROBERT, The Labrador Peninsula. Scot. Geog. Mag. 11: 335-361. 1895.
8. ———, Distribution of forest trees in Canada. Scot. Geog. Mag. 13: 281-296. 1897.
9. CLEMENTS, F. E., The development and structure of vegetation. Rep. Bot. Surv. Nebraska. VII. 1904.
10. ———, Research methods in ecology. Lincoln, Neb. 1905.
11. COOLEY, GRACE E., Silvicultural features of *Larix americana*. Forestry Quart. 2: 148-160. 1904.
12. COOPER, W. S., Reproduction by layering among conifers. BOT. GAZ. 52: 369-379. 1911.
- 12a. ———, The ecological succession of mosses, as illustrated upon Isle Royale. Plant World 15: 197-213. 1912.
13. COWLES, H. C., The physiographic ecology of Chicago and vicinity. BOT. GAZ. 31: 73-108, 145-182. 1901.
14. ———, The influence of underlying rocks on the character of the vegetation. Bull. Amer. Bur. Geog. 2: 1-26. figs. 10. 1901.
15. ———, The causes of vegetative cycles. BOT. GAZ. 51: 161-183. 1911.
16. DACHNOWSKI, A., The toxic property of bog water and bog soil. BOT. GAZ. 46: 130-143. 1908.
17. ———, The vegetation of Cranberry Island (Ohio) and its relations to the substratum, temperature, and evaporation. BOT. GAZ. 52: 1-33, 126-150. 1911.

18. DANA, S. T., Paper birch in the northeast. U.S. Dept. Agric. Forest Service, Circular 163. 1909.
19. DAVIS, C. A., Peat: Essays on its origin, uses, and distribution in Michigan. Mich. Geol. Surv. Ann. Rep. 1906 (1907).
20. FERNOW, B. E., An analysis of Canada's timber wealth. Forestry Quart. 6:337-353. 1908.
21. FINK, BRUCE, The lichens of Minnesota. Contrib. U.S. Nat. Mus. 14: viii+269+xvi. 1910.
22. FOREST SERVICE, U.S., The white spruce. Silvical Leaflet 15. 1908.
23. FOSTER, J. W., and WHITNEY, J. D., Report on the geology and topography of a portion of the Lake Superior land district, in the state of Michigan. Exec. Doc., 1st Sess., 31st Cong. 9:pt. 1. 1850.
24. ———, Report on the geology of the Lake Superior land district. Pt. II, the iron region. Sen. Doc., Spec. Sess., 32d Cong. 3:1851. Contains a list of plants of the Upper Peninsula by W. D. WHITNEY, including some from Isle Royale.
25. FOX, W. F., The Adirondack black spruce. Ann. Rep. N.Y. Forest Comm. 1895.
26. GANONG, W. F., Preliminary outline for a plan for a study of the precise factors determining the features of New Brunswick vegetation. Bull. Nat. Hist. Soc. New Brunswick 17:127-130. 1899.
27. ———, A preliminary synopsis of the grouping of the vegetation (phytogeography) of the province of New Brunswick. Bull. Nat. Hist. Soc. New Brunswick 21:47-60. 1902.
28. ———, The nascent forest of the Miscou beach plain. BOT. GAZ. 42:81-106. 1906.
29. GLEASON, H. A., The ecological relations of the invertebrate fauna of Isle Royale. In ADAMS 4. 1909.
30. GRAVES, H. S., The study of natural reproduction of forests. Forestry Quart. 6:115-137. 1908.
31. GREEN, S. B., Forestry in Minnesota. St. Paul. 1902.
32. HARSHBERGER, J. W., An ecological study of the flora of mountainous North Carolina. BOT. GAZ. 32:241-258, 368-383. 1903.
33. HOLT, W. P., Notes on the vegetation of Isle Royale, Mich., and annotated list of plants. In ADAMS 4. 1909.
34. HOWE, C. D., The reforestation of sand plains in Vermont. BOT. GAZ. 49:126-148. 1910.
35. KNECHTEL, A., Natural reproduction in the Adirondack forests. Forestry Quart. 1:50-55. 1903.
36. LANE, A. C., Geology of Isle Royale. Geol. Surv. Mich. 6:pt. 1. 1898.
37. LIVINGSTON, B. E., The relation of soils to natural vegetation in Roscommon and Crawford counties, Michigan. BOT. GAZ. 39:22-41. 1905.
38. MACMILLAN, C., On the occurrence of sphagnum atolls in central Minnesota. Minn. Bot. Stud. Bull. 9. 1893.

39. MACOUN, JOHN, Catalogue of Canadian plants. Geol. and Nat. Hist. Survey of Canada. 1883-1890.
40. ———, The forests of Canada and their distribution, with notes on the more interesting species. Trans. Roy. Soc. Canada 4:3-20. 1894.
41. MOORE, B., and ROGERS, R. L., Notes on balsam fir. Forestry Quart. 5:41-50. 1907.
42. OLSSON-SEFFER, P., Examination of organic remains in postglacial deposits. Amer. Nat. 37:785-797. 1903.
43. Ontario dept. of crown lands, Report of the survey and exploration of northern Ontario. 1900 (1901).
44. PINCHOT, G., and GRAVES, H. S., The white pine. New York. 1896.
45. Quebec dept. of lands and forests, The regions of Quebec, Lake St. John, Chicoutimi, and of the north shore of the St. Lawrence. 1908.
46. ———, Report of the minister of lands and forests of the province of Quebec. 1909 (1910).
47. ROBINSON, B. L., and FERNALD, M. L., GRAY'S Manual of botany. Ed. VII. New York. 1908.
48. ROTH, F., On the forestry conditions of northern Wisconsin. Wis. Geol. and Nat. Hist. Surv. Bull. (Economic ser.) no. 1. 1898.
49. RUTHVEN, A. G., Notes on the plants of the Porcupine Mountains and Isle Royale, Michigan. In ADAMS 3. 1906.
50. SARGENT, C. S., Manual of the trees of North America. Boston and New York. 1905.
51. SCHWARZ, G. F., The sprout forests of the Housatonic Valley of Connecticut. Forestry Quart. 5:121-153. 1907.
52. SHAW, C. H., The development of vegetation in the morainal depressions of the vicinity of Woods Hole. BOT. GAZ. 33:437-450. 1902.
53. STUPART, R. F., The climate of Canada. Scot. Geog. Mag. 14:73. 1898.
54. TRANSEAU, E. N., On the geographic distribution and ecological relations of the bog plant societies of North America. BOT. GAZ. 36:401-420. 1903.
55. ———, Forest centers of eastern America. Amer. Nat. 39:875-889. 1905.
56. ———, The bogs and bog flora of the Huron River Valley. BOT. GAZ. 40:351-375, 418-448. 1905; 41:17-42. 1906.
57. ———, Successional relations of the vegetation about Yarmouth, N.S. Plant World 12:1-11. 1909.
58. WHEELER, W. A., Notes on some plants of Isle Royale. Minn. Bot. Stud. 2:619-620. 1901.
59. WHITFORD, H. N., The genetic development of the forests of northern Michigan. BOT. GAZ. 31:289-325. 1901.
60. ZEDERBAUR, C., The light requirements of forest trees and the methods of measuring light. Forestry Quart. 6:253-262. 1908.